

Review



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Animal behaviour

Vocal matching: the what, the why and the how

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Over the years, vocal matching has progressed beyond being an interesting behavioural phenomenon to one that now has relevance to a wide range of fields. In this review, we use birds and cetaceans to explain what vocal matching is, why animals vocally match and how vocal matching can be identified. We show that while the functional aspects of vocal matching are similar, the contexts in which matching is used can differ between taxa. Whereas vocal matching in songbirds facilitates mate attraction and the immediate defence of resources, in parrots and cetaceans it plays a role in the maintenance of social bonds and the promotion of behavioural synchrony. We propose criteria for defining vocal matching with the aim of stimulating more matching studies across a wider range of taxa, including those using other, non-vocal, communication modalities. Finally, we encourage future studies to explore the importance of vocal learning in the development of vocal matching, and the information it may provide to third parties in the communication network.

1. Introduction

Vocal matching is a distinctive interactive signalling behaviour occurring over short, possibly signal-by-signal, timescales. It has been used in animal communication studies to indicate how birds perceive categories of song variation, how cetaceans interact at long range and to infer aspects of social cognition, e.g. negotiation of territory boundaries in songbirds and individual addressing in dolphins. The strategic use of vocal matching to address others (e.g. social companions, territorial neighbours) requires animals to control their vocal response to match the acoustic features of a signal just heard by changing features of their elicited response. How animals achieve immediate matching of signals, when underlying cognitive and neurological mechanisms may differ markedly between species, is an aspect of vocal matching as an interactive signalling behaviour that draws significant attention from researchers across the disciplines of ecology, cognition, behaviour, neurophysiology and evolutionary biology.

In this review, we address three main themes. First, we explain *what* vocal matching is, using cetacean and bird examples that characterize this remarkable vocal behaviour. We also evaluate the case for restricting the use of the term to interactive, near immediate—i.e. signal-by-signal—matching. Second, we consider *why* animals vocally match, exploring mechanistic and functional aspects using the same cetacean and bird examples. Third, we explore *how* researchers can identify vocal matching, focusing on recent advances in playback experiments and statistical techniques. While we consider vocal signals, we recognize that very similar characteristics apply to acoustic signals that are not produced by the vocal organ. We therefore consider the extent to which concepts analogous to vocal matching can be extended to taxa using other modalities for communication.

Table 1. Criteria for identifying signal matching in animal communication systems.

criterion	definition
signal match	the signal emitted by animal B is a match of the signal emitted by animal A, i.e. signal features (e.g. frequency and time parameters in vocal signals) are the most similar in animal B's repertoire. Note that the similarity of the match may depend on the perception and salience of signal parameters to the animals
timing interval	the match is emitted by animal B within a short time of the original signal produced by animal A. This will be true if the match is the first signal emitted by animal B upon hearing animal A's original signal and if the interval between the signals is similar to the inter-signal interval when an animal is not involved in an interaction
non-random pattern	matching should occur above random levels (determined by signal repertoire size, sharing rate and signalling rate—see §4)

2. The *what*: key features of vocal matching and a working definition

(a) Vocal matching in birds and dolphins

Most species of songbird have a repertoire of functionally equivalent song types, i.e. they sing more than one version of the species-specific song. An exemplar is the great tit (*Parus major*), whose song consists of a phrase, commonly of two elements, repeated several times. Song types are categorized on the basis of the morphology of the repeated elements. Song-type matching (also referred to as song matching or matched counter-singing) occurs when a repplier sings the same song type as an initiator. Great tits, on average, sing a repertoire of three song types, and males share about one song type with each of their neighbours [1,2]. Playback of a song from an individual's repertoire elicited song-type matching—and also close approach to the playback loudspeaker [3]. Vocal matching in songbirds was first reported in the mid-twentieth century [4,5]. It is not universal [6], but many species, e.g. song sparrows (*Melospiza melodia*; [7,8]) and banded wrens (*Thryothorus pleurostictus*; [9]) are known to match playback. Song-type matching has clearly been shown to be a signal of aggressive intent, used by males to establish and maintain territory boundaries during the breeding season [10].

Vocal matching has also shed light on individual addressing in dolphins. The common bottlenose dolphin (*Tursiops truncatus*) has a large and varied whistle repertoire, and is known to immediately match whistle types (i.e. the pattern of frequency modulation over time) during vocal exchanges [11–13]. These matching interactions often involve their signature whistles [14]: a learned individually distinctive signal that encodes the identity of the animal in the frequency modulation pattern of the whistle, independently of general voice features [15]. Although each signature whistle is predominantly used by one individual [16], dolphins will occasionally copy each other's signature whistle [13,17,18]. Signature whistle copies are produced in vocal matching interactions, whereby the owner of the whistle produces its signature whistle first, and then a second individual produces a copy of that whistle immediately after the owner [11,13]. The rapid matching of other whistle types, i.e. non-signature whistles, has also been shown to play a significant role in bottlenose foraging behaviour [12].

Interestingly, vocal matching has also been documented in parrots, many species of which are known to form fission fusion societies, and thus likely face the same social pressures as dolphins. In fact, like bottlenose dolphins, the immediate matching of contact calls in orange-fronted conures (*Eupsittula canicularis*) facilitates the affiliative addressing of individuals [19].

(b) Defining vocal matching

These examples show two key features of vocal matching: it is an interactive process driven by the internal decision-making of the individuals involved, and it occurs at above chance levels. However, the term vocal matching has been applied to a range of vocal behaviours. For example, it has been suggested that shared calls, such as those used for group membership are, by definition, matched calls [20]. Similarly, many animals share signals, and as a result, it is not uncommon for animals to produce the same signals simultaneously, i.e. signals co-occur without interaction.

Individuals may also produce the same signal as a result of an external stimulus; such context calling will result in apparent vocal matching, but it does not involve any interaction between individuals [21,22]. Interactive vocal behaviour over longer time scales has also been referred to as matching, albeit qualified (e.g. *delayed matching* [9] and *repertoire matching* [23]). To ensure that considerations of what, why and how are applied to the same phenomenon, both in this review and when expanding discussion to other taxa and signalling modalities, we propose that immediate vocal matching requires three criteria (table 1).

Establishing that these criteria have been met can be challenging. We discuss techniques suitable for doing so in §4.

3. The *why*: functions and mechanisms underlying vocal matching

(a) Functions

There is experimental evidence for two functions of matching: (i) to direct vocalizations to a particular receiver and (ii) reciprocal exchange of information on range (i.e. separation distance). Here, we discuss the evidence for both of these functions.

(i) Addressing another signaller

A consequence of communication occurring in a network (argued to be both ubiquitous and ancestral [24]) is that signallers must change aspects of their signalling behaviour if they wish to address a particular individual receiver rather than all receivers in the network. A number of features of bird song can be changed interactively, often song by song, to more precisely indicate the intended receiver. As previously explained, most songbirds sing a repertoire of song types and song-type matching could function to address a rival [25]. However, in many species, repertoire sizes are modest (fewer than 25 song types), repertoire sharing is limited, and song types are sung with eventual variety,

resulting in limited scope for an addressing function of song-type matching. Within a bout of the same song type, song length can be varied song by song. Matching song length could therefore provide a more specific indication of the intended receiver than song-type matching because it does not depend on the singers sharing song types (although it may be easier to match song length if singing the same song type) and it can be changed song by song. Singers can also vary when each song is produced in relation to another singer—often referred to as delay in song-birds. An immediate reply (minimal delay) can potentially give the most unequivocal and general indication of the interacting singers, because a response to a song is independent of the song type and song length [26,27]. Interactive playback provided evidence that song-type matching, song-length matching and delay formed a successively more precise indication of the intended receiver in great tits [28].

Vocal matching has a similar addressing function in both parrots and dolphins [19,29]. Interactive playback experiments with dolphins show that when an individual produces its signature whistle, and another individual immediately replies with a copy of that whistle, then the initiator emits its signature whistle again, as if addressed [29]. The initiator does not respond in this way if the replier produces a different whistle type. This pattern for signature whistle matching holds true across sexes and ages [29]. If the whistle match is produced within 1 s of the original signal, then the initiator always replies [29], emphasizing the importance of the timing criterion in our definition (table 1). Playback experiments with orange-fronted conures revealed that individuals also immediately imitated contact calls to address specific individuals [19].

(ii) Range information exchange

Birds are known to be able to range, i.e. use the extent of song degradation (accrued during the song's transmission through the habitat) to estimate the distance to the singer [30]. However, they are better able to do this if they are familiar with the song type [31,32]. Therefore, by choosing to match song types a replier is (i) facilitating ranging by providing the initiator with a familiar song type through song-type matching; (ii) providing information that it can range the initiator's song (because matching demonstrates the replier's familiarity with the initiator's song type). Therefore, this could be considered a form of mutual, or reciprocal, information exchange [30].

The idea that dolphins or other Odontoceti use vocal matching as a means of exchanging information on range remains more speculative. For example, killer whales (*Orcinus orca*) have a group-distinctive repertoire of intense stereotyped calls and will commonly vocally match these shared calls when out of visual range [33], with the mixed-directionality of these calls providing cues to the distance and/or orientation of the calling animal, as a means of promoting group cohesion and synchrony [34]. The matching of shared whistles on the foraging patch by bottlenose dolphins [12] may function in a similar way, allowing them to signal their current positions and/or intended movement trajectories [33,34].

(iii) Strengthening social bonds

A potential third function of matching, which has not been experimentally tested, is the strengthening of social bonds. For example, in sperm whales (*Physeter macrocephalus*), the

matching of codas (stereotyped patterns of broadband clicks) primarily occurs during social periods when animals are in visual contact [35]. It has been suggested that coda matching helps reinforce social bonds between whales [35], and this is a nice example of immediate vocal matching used in a social context. However, other examples are less clear. Evidence suggests that animals will produce acoustically similar calls as a means of social affiliation, but there is no evidence that this constitutes a form of vocal matching. Instead, it may reflect context calling with shared calls where animals converge to vocally accommodate one another, e.g. chorusing [36], thus falling outside of our definition of immediate vocal matching. Techniques used to test for immediate vocal matching are discussed in §4.

(b) Mechanisms

The underlying mechanisms involved in immediately matching a conspecific are worth considering, as they may be very different between species. For matching to occur, animals may have to possess some knowledge of the acoustic model they wish to match. Vocal matching is therefore subject to two information constraints, the first being that the signaller has paid attention to the original signal produced by the previous caller, and the second that the signaller can reproduce a sufficiently similar signal [10]. Thus, an animal's ability to partake in matching may be the result of either possessing a mechanism to assess what sound in their shared repertoire is the most similar and producing that, or the facility to immediately imitate a novel sound that is not in their repertoire. Such spontaneous vocal mimicry is, however, likely to be rare and limited to those species capable of vocal production learning [37] that can learn novel signals even as adults; e.g. bottlenose dolphin [38], beluga whales (*Delphinapterus leucas*; [39]), great tits [40], orange-fronted conures [41] and African grey parrots (*Psittacus erithacus*; [42]).

We know that bottlenose dolphins and orange-fronted conures are adept vocal mimics that can produce almost perfect copies of novel acoustic signals after only one exposure [38,41], and therefore, both species seem capable of generating very similar calls *de novo*. It is therefore conceivable that both dolphins and parrots are able to copy the calls not just of social companions, but also of strangers [13,41]. However, with regard to dolphins, because signature whistle copying only occurs between social companions [13], it is perhaps unlikely that strangers would be matched. Instead signature whistle matching appears to be used by animals to strengthen social relationships [13] or to facilitate the localization of specific individuals in large social networks [11,29,43]. So, although dolphins may learn the signature whistles of individuals within their wider social network, only the signature whistles of close social affiliates are routinely copied. Thus, if an individual only has to match the whistle of a social companion, then the demands on the learning system may be considerably reduced.

Other species may only copy new sounds if they fit within species-specific parameters [44,45]. In these instances, rather than spontaneous imitation, animals are likely to rely on memory of their shared repertoire in order to vocally match. Many songbird species have small-to-moderate repertoire sizes; therefore, the number of song templates to choose from in order to match a neighbouring male is small. However, the importance of matching may explain patterns

of learning by adult great tits [40]. Other species, with repertoires of well over 100 song types, also song-type match; e.g. tropical mockingbird (*Mimus gilvus*; [46]), marsh wrens (*Cis-thorus palustris*; [47]) and sedge wrens (*C. platensis*; [48]). In such species, song-type matching presents the challenge of quickly retrieving the appropriate song from a large repertoire [46]. Songbirds with large repertoires may produce song types in stereotyped sequences [49], which could prime birds as to which song a neighbour will sing next, facilitating song-type matching [46]. Songbirds that sing with immediate variety, where successive songs are different, may divide their song repertoire into subsets, reflecting a hierarchical organization of song-type memories, which can both aid the decision-making process of what song to sing next and can facilitate subsequent song retrieval from memory [49–51], both of which help facilitate vocal matching.

4. The *how*: identifying vocal matching

(a) Observational approaches

Identifying a vocal exchange as vocal matching requires that the response is the most similar in the repplier's repertoire (table 1). This necessitates sufficiently lengthy observations to characterize the subjects' repertoires. Furthermore, the experimental design needs to discount the occurrence of alternative explanations such as context calling (§2). This is particularly important for parent–offspring exchanges, where mother and offspring can either use a shared contact call or individual vocal signatures to maintain contact. The former may be confused with vocal matching; however, if that is the only signal used between mother and offspring, then we may expect signal production to also occur at random levels. An understanding of the vocal repertoire is therefore important, coupled with the techniques available to identify vocal matching, which we explore in the following sections.

(b) Experimental approaches

Researchers have long used playback experiments to determine if animals are capable of vocal matching, and to elucidate its function. Interactive playback experiments, where the sound played back is determined by the focal animal's current vocal behaviour, have been particularly pivotal in this area (see [52] for a recent review). These types of experiments allow us to explore the interactive features of signal exchanges that include vocal matching [28], and have provided key insights into the signaller's behaviour when matching (i.e. sender's perspective [8,9]) and the receiver's response to being vocally matched (i.e. receiver's perspective [53–55]). Interactive playback experiments also allow the researcher to investigate the context in which matching may occur by using carefully chosen experimental controls (e.g. male songbirds will match strangers, which are a greater perceived threat, more often than neighbours [56,57]). They are also useful for investigating time-specific responses that are salient to the animal during vocal matching exchanges [29].

(c) Statistical approaches

To meet the criterion that vocal matching is a non-random interaction (§2), randomization tests can be used to determine whether vocal matching in natural interactions occurs at above chance levels by comparing the observed number of matches

with the expected if calling were random. The test preserves call timing and can be used alongside a bout analysis to test for matched counter-calling within each bout. Controlling for the context-specificity of an animal's calling behaviour is important as many animals do not call continually, but vocal production tends to occur in short bursts (bouts). A bout analysis using log-frequency and nonlinear least-squares [58,59] can validate the presence, or otherwise, of vocal matching within the context of natural patterns of calling behaviour. The bout criterion is defined as the time that separates intervals within a bout from intervals between bouts [60], and, once identified, each bout can then be treated separately [33]. To summarize, by using statistical approaches and delineating a short time window in which two calls of the same type have to occur to be considered a match, studies are able to distinguish vocal matching from the simultaneous, but non-interactive, production of shared call types (e.g. context calling [11,13,33,35]).

5. Conclusion

Immediate vocal matching can be either affiliative, as shown in parrots and dolphins, or aggressive, as demonstrated with songbirds. However, on a broader level, it is a potentially universal means of addressing, as discussed in [29,36], that allows animals to share information on distance, to establish territorial boundaries and to strengthen social bonds. It remains fascinating, because although the cognitive or neurological basis of matching may differ, it is used by individuals from different taxa to help mediate male contests, group separations and relationships between social affiliates. By proposing robust criteria to identify signal matching (table 1) and the techniques to study them (§4), we hope to give impetus to matching studies in a wide range of taxa and signal modalities.

One key area to be investigated is the role of learning. Our criteria will allow researchers to determine if vocal matching occurs in a variety of species, or only in those that use learned signals, such as songbirds, parrots and cetaceans. Given that vocal learning has been discussed as a prerequisite for the evolution of spoken language [61], an understanding of the prevalence and evolutionary roots of matching may shed light on the origins of language.

A second area of interest to consider is how third parties perceive vocal matching, and what information they obtain from such vocal interactions. Within a communication network, vocal matching can occur between competitors (i.e. songbirds) or social affiliates (i.e. dolphins and parrots). Eavesdropping by third parties on song-type matching between male songbirds has been shown to play an important role in female mate choice in black-capped chickadees (*Poecile atricapillus*) [62] and in the vocal development of juvenile song sparrows [63]. It remains unclear what information third parties may gain from eavesdropping on matching interactions in bottlenose dolphins. As signature whistle matching appears to only occur between close social affiliates [13], eavesdropping on matching interactions may help inform individuals about the strength of third-party relations. This may be particularly important in those dolphin populations characterized by high levels of cooperation and conflict [64].

Finally, whether similar considerations to those discussed above for vocal matching can apply to interactive signalling in other modalities is an important area for research. Visual signal matching may be an excellent candidate, with evidence

suggesting that wolf spiders (*Schizocosa ocreata*) adjust their visual courtship displays to match the performance of rivals [65]. While features of many modalities will allow the criteria to be met, a possible exception is chemical signals, where rapid patterning may not be achievable [66], and the time-scale for interactive signalling is likely to be more extended.

Extending studies of signal matching to other modalities will help to determine if its role in communication behaviour is general.

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